XXIII. Xanthorhoë ferrugata (Clerck) *and the Mendelian Hypothesis.* By Louis B. Prout, F.E.S.

[Read December 5th, 1906.]

About ten to twelve years ago, consequently some time before I first made acquaintance with Mendel's theory, I undertook some rather extensive heredity experiments upon *Xanthorhoë* (*Coremia*) *ferrugata*, Clerck, generally known to British entomologists as *Coremia unidentaria*, Haw., a common little Geometrid species which exhibits very definite colour dimorphism. A tolerably full account of the results I obtained has already been published in the "Transactions of the City of London Entomological Society" for 1897–98, pp. 26–34, but as that periodical has had but a limited circulation, and as, for obvious reasons, I made no reference to the relation of the experiments to the views of Mendel, I make no apology for republishing the main outlines.

The synonymy of this species and its closest relative, *X. spadicearia* (Schiff.), Bkh. = *ferrugaria*, Haw., has been much confused, and is almost unintelligible in most of our catalogues, but will be found clearly set forth in Meyrick's "Handbook of British Lepidoptera," p. 229. The only fault there is that Meyrick omits to mention that the purple-banded form is the "type" of both Clerck and Linnæus, and occurs (though sparingly) in Britain as well as "abroad," while the black-banded form is the ab. (et var.) *unidentaria* of Haworth. For the purpose of the present paper it will be sufficient to speak of the type as "purple" and the aberration as "black," thus avoiding any tax on the memory of those who may not be familiar with the complexities of the synonymy.

There is no doubt that, in Britain, the black is the "dominant" form, in the ordinary acceptation of the word, and without postulating any Mendelian application. I have repeatedly bred from wild black females and have invariably obtained therefrom black specimens only, sometimes carrying on the strain for two or three generations. Many friends have had the same result, and so has the

German entomologist Fuchs, who—on account of this "epigonic" evidence—recently proposed to erect the form as a distinct species under the name of *eximiata* (*fide* R. Püngeler). The var. *stupida* of Alphéraky, from Central Asia (No. 3370*a*, in Staudinger's "Catalog") is also invariably black-banded, so far as I have been able to learn; and a series which I have, through the kindness of Mr. F. H. Wolley Dod, received from Calgary, Alberta, shows the same stability of colour. The very few recorded cases of breeding purple examples among broods raised from wild black females may therefore pretty safely be taken as indicating mongrel origin—"hybrids" in the Mendelian sense—the male parent being assumed to have been purple-banded.

I know of no locality where the purple form entirely ousts the black, but I understand from Dr. R. T. Cassal that the first-named is the more frequent in the Isle of Man. Further, wild purple specimens have nearly always yielded a percentage of black in the progeny. The most important exception known to me was a considerable brood reared by my friend Herr Rudolf Püngeler, at Aachen.

Coming now to the heredity experiments, I may say that the whole of the material which is of any significance for present purposes was obtained from a single locality, Sandown, Isle of Wight, where both forms (purple and black) occur together, with a considerable preponderance of the black. I have reared isolated broods from other British localities, which have merely tended to confirm the general results.

From various causes, set forth in my earlier paper, I was unable to work as systematically as I could have wished. The resistance of this species to any continuous inbreeding is more pronounced than in any other case which has come under my notice, and many attempted crossings failed utterly, while many others yielded so few specimens as to be practically valueless for statistical purposes. I shall, in consequence, almost confine consideration to the larger broods, referring those who desire more detailed information of the rest to the aforementioned "Transactions of the City of London Entomological Society."

Black × Black.—Taking these first, as I have called them "dominant," I find there are four batches to be

considered; these produced respectively 16, 22, 17 and 27 imagines, and *all* were black with the exception of a single intermediate * in the brood of 22. In this brood, and also in that of 27, the paternal grandmother was black, the maternal purple; in the other two, the reverse was the case; in no instance was a male grandparent known, as all were second generations from wild females. It is interesting, too, that in one of the broods which almost failed, the only four imagines that developed were black, notwithstanding that both the parents (black) were the offspring of a purple female. Practically therefore, black × black could be depended upon to breed true, whatever the ancestry.

Black × Purple.—Five broods give the following results: (1) 42 black, 27 purple; (2) 37 black, 32 purple, 4 intermediate; (3) 36 black, 31 purple; (4) 49 black, 47 purple; (5) 7 black, 10 purple. This gives a total of 171 black, 147 purple, 4 intermediate; or respectively (omitting fractions) 53 per cent., 45 per cent., 1 per cent.

The brood which shows the greatest disparity in the representation of the two forms—numbered (1) above—had the ♂ parent black and the ♀ purple, while in the other four cases the sexes were reversed; but I am not inclined to attach much weight to this slight discrepancy. The pedigree, so far as known, was as follows: (1) paternal grandmother black, maternal purple; (2) and (3) *vice versâ;* (4) ♂ parent a wild purple specimen, ♀ parent (black) the offspring of black ♂ and ♀, which, in their turn, sprang of captured purple and black females respectively; (5) both parents (brother and sister) the offspring of a captured purple female.

Purple × Purple.—I reared nine of these broods, mostly with somewhat complicated pedigree, as I was especially interested in attempting to eliminate the black element by selection; that I failed in this attempt, the following figures will show. Six of the broods were large enough, numerically, to be taken into account:† (1) 52 purple, 21 black (♂ parent purple, wild; ♀ parent purple,

* Real intermediates are, in my experience, of exceedingly rare occurrence; I have only reared 10 which can be so regarded, amongst considerably over 1000 specimens—*i. e.* less than one per cent.

† Even the few specimens reared in the remaining three cases showed, in each instance, at least one black specimen.

bred from purple × purple, these being brother and sister reared from wild purple female). (2) 37 purple, 9 black, 1 intermediate (♂ parent purple, from a wild purple female; ♀ parent purple, a member of the brood just described as (1)). (3) 6 purple, 11 black (♂ parent purple, from a wild purple ♀; ♀ parent purple, likewise from a wild purple ♀). (4) 13 purple, 2 black, 1 intermediate (♂ parent purple, from wild purple ♀; ♀ parent purple, from wild purple ♂ × black ♀, the latter the offspring of black ♂ and ♀, which, in their turn, sprang from wild purple and wild black ♀ respectively). (5) 13 purple, 8 black (♂ parent purple, from a wild purple ♀; ♀ parent purple, likewise from a wild purple ♀). (6) 16 purple, 7 black (♂ parent purple, from wild purple ♀; ♀ parent purple, from the brood just noticed as No. (3)). These figures give a total for the six broods, of 137 purple, 58 black, 2 intermediate; or respectively (omitting fractions) 69 per cent., 29 per cent., 1 per cent. It will be observed that in one case, No. (3), the black form actually preponderated, notwithstanding a known purple ancestry for two generations; in the other five, the percentage of black varied from 38·1 per cent. to 12·5 per cent. approximately.

It will be at once manifest, that the weakness of the above statistics for the purposes of elucidation of Mendelism consists in the almost constant necessity of introducing wild stock of unknown pedigree. Nevertheless, the "discontinuity" of the two forms and the apparent "purity" of most members of the black race give sufficient impression of a "Mendelian species" to justify my offering a few comments.

I cannot refrain from remarking, in the first place, that if only certain species are "Mendelian" in their behaviour —as seems to be hinted by some writers, *e. g.* Doncaster in "Ent. Record," xviii, p. 249—it would, to me, be a grave argument against our attributing the Mendelian phenomena, when observed, to any deep-seated biological cause; it is inconceivable that, among organisms so homogeneous as the various species of Lepidoptera—or even Insecta—there could be cytological differences vast enough to allow of gametic purity in certain cases only. Probably, however, it may be a sufficient reply that all species are really alike "Mendelian" in vital organization, but that it by no means thence follows that a particular manifestation of

dimorphism which appeals to the human eye—*e. g.* of coloration, as in our *Xanthorhoë*, is necessarily correlated to the true gametic differentiation. This is, at least, a possible interpretation of Doncaster's words (*loc. cit.*) that in some cases, such as that of the melanism of *Aplecta nebulosa*, "the inheritance is not Mendelian."

The only in-bred broods of which I reared any imagines deserve mention here, in spite of their small numbers. (1) From a wild purple ♀, which produced 21 black, 15 purple, and one intermediate in her progeny, a pairing of two of the purple examples was obtained. From this pairing, 10 purple and 2 black were reared, none of which were successfully paired together. (2) From another wild purple ♀, which produced 9 black and 4 purple, a pairing of two of the black was obtained. From this there resulted only 4 imagines, all of which were black. Again the strain failed at this point. (3) From a third wild purple ♀, which produced 5 black and 8 purple, a pairing of purple ♂ with black ♀ was obtained. This pairing resulted in the brood of 7 black and 10 purple, which has already been alluded to as "black × purple, No. 5." Yet again the strain failed at this point.

Neither of these results seems to suggest with any clearness that either form was a "recessive"; one looks in vain for any approximate 3 : 1 ratio, such as might have been expected, by the ordinary laws of chance, even when allowance had been made for the large percentage of loss in rearing. Rather do they suggest some kind of biometric interpretation, and with the potency of each colour approximately equal (or black somewhat the stronger) and equally direct in its effect. In the case numbered (1), a brood in which $\frac{5}{12}$ were purple, gave, in the next generation and by the aid of purple selection, $\frac{10}{12}$ purple, or just double the percentage. In that numbered (2), a brood in which $\frac{9}{13}$ (69 per cent.) were black, gave one, by black selection, in which one hundred per cent. were black. In that numbered (3), where there was a cross-pairing of the two colours, the percentages in the two generations were very little disturbed, working out (roughly) at 38·5 per cent. and 41·2 per cent. of black specimens respectively.

It remains to consider whether the larger experiments detailed earlier in this paper throw any further light on the statistical aspects of the question. It is manifest from the figures I have given, that there has been no behaviour

analogous to that of Mendel's classic "round" and "angular" peas, or Raynor's *Abraxas grossulariata* and ab. *flavofasciata* (cfr. "Ent. Record," xv, pp. 142–144); no case, that is to say, in which a crossing of the two colours has resulted in the appearance of a first generation manifesting one colour only (Mendel's "Dominant.") This, I apprehend, is not necessarily fatal to the application of the Mendelian hypothesis, as it is always conceivable that none of the pairings may have happened to be made with sufficiently pure stock; assuming the black to be the dominant colour, it is still not impossible that all those which were mated with purple specimens chanced to be really "hybrids" in their organization, and in this event a part of the latent purple element in them should, in fertilization, meet the purple element of the "recessive," and result in specimens of that colour. But it seems to me improbable that this should always have happened, considering the number of pairings obtained; it must be remembered that hybrids only outnumber pure dominants in the proportion of 2 : 1.

Further, I do not see how to account for the reappearance of black specimens in all my considerable broods of purple × purple. If the recessive colour appears only in pure recessive individuals, two of such, when mated, should always breed true. And following the same line of thought, one feels that the black pairings ought *not* to breed true with the persistence which experience has revealed; for two-thirds of them ought to be veritable "hybrids" with simply an external dominant character.

Taking all the facts into consideration, it thus appears demonstrable that the colour dimorphism of *Xanthorhoë ferrugata* does not obey Mendelian law. If there is any correlation at all between the colouring and gametic purity, it must be of so involved a nature as to baffle our present powers of discernment. For instance, it is possible, on certain analogies which might be adduced, that the dominant form of this species may be a constantly black or a constantly purple one, and the "recessive" a variable one in colour, one of its forms being indistinguishable—so far as the human eye is yet trained—from the "dominant." Or conversely, the recessive may be constant to one colour and the dominant variable. To me, however, the simplest view is still that which I deduced from my work at the time when it was undertaken, and

which I have mentioned in this paper as supported by the very few successful experiments of actual inbreeding; namely, that in this species there is in general a "*very direct* response to immediate parentage, especially if black; black × black producing black only (irrespective of ancestry), red × red producing over two-thirds red, red × black roughly half and half, or black slightly in the ascendant" ("Trans. City Lond. Ent. Soc. for 1897–8, p. 30"; of course "red" in this quotation corresponds to "purple" of the present paper). If I could learn how to inbreed it for a few generations with even tolerable success, I should be strongly tempted to resume my experiments upon it, with a view to definite biometric work; I am decidedly of opinion that with a little more practice and experience, it would be possible to forecast almost exactly the percentages of the two colours in a given brood of known parentage.